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Large mammals from Rickenbach (Switzerland, reference locality MP29, Late Oligocene): biostratigraphic and palaeoenvironmental implications

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Abstract Since the first exploitation of the Huppersandstones quarry of Rickenbach (Canton Solothurn, Switzerland) in 1898, many fossils of plants, molluscs, and vertebrates have been discovered. The study of the small mammals brought this locality to international recognition as the type locality for the European mammalian reference level MP29 (latest Oligocene). Our study reviews the terrestrial herbivorous mammals of Rickenbach and aims to reconstruct the palaeoenvironmental and palaeoclimatic conditions in which they lived. The perissodactyls and cetartiodactyls are described and identified: *Protapirus* sp. (Tapiridae), *Ronzotherium romani* and *Diaceratherium lamilloquense* (Rhinocerotidae), *Anthracotherium magnum* and *Microbunodon minimum* (Anthracotheriidae), *Palaeochoerus pusillus* (Suoidea), and *Dremotherium guthi*, "*Amphitragulus*" *quercyi*, "*Amphitragulus*" *feningrei*, and *Babameryx engesseri* gen. et sp. nov. (Ruminantia). Based on the updated faunal list, a cenogram of the locality of Rickenbach is established. We also performed ecomorphologic analyses on ruminants and rhinocerotids. The reconstructed palaeoenvironment of Rickenbach probably corresponded to a savannah woodland affected by a subtropical climate with clear seasonality.

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Abbreviations

C/c	Upper/lower canine
D/d	Upper/lower deciduous teeth
I/i	Upper/lower incisor
M/m	Upper/lower molar
P/p	Upper/lower premolar
Mc	Metacarpal
Mt	Metatarsal
H	Height
L	Length
W	Width
APD	Anteroposterior diameter
TD	Transverse diameter
GI	Gracility index
HI	Hypsodonty index

Introduction

Since its discovery in 1897, and until it was recognised as the type locality for the European mammalian reference level MP29 by Schmidt-Kittler et al. (1987), Rickenbach (Canton Solothurn, Switzerland) has become one of the most important mammal localities in Western Europe. Additionally, Rickenbach is also:

- A locality studied by the "Basler School", from Hans Georg Stehlin to Johannes Huerzeler, and later Burkart Engesser,
- Number CH/1088/2 in the "Register of the Tertiary Mammal-Bearing Localities of the Naturhistorisches

Museum Basel" created and completed by J. Huerzeler, and later by B. Engesser,

- Rickenbach, Huerzeler, and Engesser, three names related to one small mammal, *Eomys huerzeleri*, the largest Eomyidae of the Oligocene, erected by Engesser in 1982 from Rickenbach.

It is a great pleasure for us to present this locality, where our dear colleague Burkart Engesser conducted a great part of his research, especially for its recognition as an international mammal level. We hope that he will enjoy this study, which shows that the large mammals of Rickenbach fully confirm the international interest of the locality. The present paper aims to describe the ungulate assemblage, spanning the orders of the perissodactyls (tapirids, rhinocerotids) and cetartiodactyls (anthracotheriids, suoids, ruminants), and to reassess the faunal list (Table 1) and the environmental significance of Rickenbach. The geological context is presented in Fig. 1, and Fig. 2 illustrates the stratigraphic frame.

Historical background

The Rickenbach locality (Canton Solothurn, Switzerland) was a quarry mined in the first half of the 20th century to provide raw material (Huppersande, Eocene) for industrial production. Discovered by chance in 1897, the Huppersandstones were first exploited by the Glutz family (between 1898 and 1907), and then by the firm Kamber Bau AG until 1947. In 1956, the quarry was bought by the firm Hunziker for the deposit of construction waste. In 1964, the area was filled and covered with humus in order to create a biotope (Solothurnische Naturschutzverband). The "Biotopstiftung des Portlandcementwerk" was set in 1980, and is today managed by the "Biotop Stiftung Huppergrube" (since 2002). As a geological site, the quarry was included in 1996 in the "Inventar der geowissenschaftlichen schützenswerten Objekte des Kantons Solothurn" (under the number Ingeso-ooid 220), and more recently in the "Inventory of Geotopes of National Importance" (Number GIN 1201, see Berger et al. 2011).

On the 8th of July, 1905, and after several years of exploitation, R. Martin and H. G. Stehlin discovered the first fossil vertebrates in Rickenbach, associated with leaves and unionid bivalves (Martin 1906). The first geological profiles and pictures were documented by Martin (1906), Rollier (1910), Kehrer (1922), and Baumberger (1927). Additionally, a faunal list was established by Stehlin (1914). During the years 1916–1924, several collectors and palaeontologists (e.g., G. Schneider, E. Kuhn, J. Huerzeler) brought an important quantity of material to H. G. Stehlin. The latter stored most of these fossils in the Naturhistoriches Museum Basel, and many publications were edited (Helbing 1922, 1928; Kehrer 1922; Stehlin 1922; Schaub 1925, 1933; Baumberger 1927). A second important excavation was carried out in 1935, as attested by Froehlicher (1935) and Erni and Kelterborn (1948). A

Table 1 Updated floral and faunal list of Rickenbach (MP29, Switzerland)

Mammalia	*Microbunodon minimum* [a]
Amphiperatherium exile	*Anthracotherium magnum* [a]
Talpidae indet.	*Palaeochoerus pusillus* [a]
Amphechinus sp.	*Caenotherium* sp1
Dinosorex huerzeleri	*Caenotherium* sp2
Gliravus buijni	*Dremotherium guthi* [a]
Microdyromys cf. *praemurinus*	*"Amphitragulus" quercyi* [a]
Sciurus sp.	*"Amphitragulus" feningrei* [a]
Steneofiber dehmi	*Babameryx engesseri* n.g. n.sp. [a]
Rhizospalax poirrieri	**Plantae**
Eomys cf. *ebnatensis*	*Pinus* cones
Eomys huerzeleri	Alnoid leaves
Adelomyarion vireti	Cinnamomoid leaves
Eucricetodon praecursor	Salicoid-Myricoid leaves
Eucricetodon cf. *dubius*	Palm leaves
Melissiodon cf. *quercyi*	**Mollusca**
Plesiosminthus promyarion	*Plebecula ramondi*
Archaeomys helveticus	*Cepaea rugulosa*
Archaeomys arvernensis	*Parachloraea oxystoma*
?Archaeomys laurillardi	*Melanopsis acuminata*
Issiodoromys pseudanoema	*Neritina* sp.
Hyaenodon aff. *compressus*	*Limnaea (Radix) subbullata*
Hyaenodon filholi	*Limnaea (Radix) subovata*
Cephalogale sp1	*Limnaea pachygaster*
Cephalogale sp2	*Planorbis (Coretus) cornu*
Amphicyon sp.	*Unio (Iridea) subflabellatus*
Haplocyon sp.	*Unio vogti*
Plesictis sp.	*Unio inaeguiradiatus*
Stenogale sp.	**Pisces indet.**
Viverridae indet.	**Reptilia**
Ronzotherium romani [a]	Testudinidae indet.
Diaceratherium lamilloquense [a]	Crocodilia indet.
Protapirus sp. [a]	**Aves indet.**

[a] Taxa reviewed in this study; other data are taken from the literature (Rollier 1910; Kehrer 1922; Stehlin 1922; Baumberger 1927; Helbing 1928; Erni and Ketelborn 1948; Viret and Zapfe 1951; Engesser 1982; Engesser and Mayo 1987; Mödden 1993; Engesser and Mödden 1997; Mödden and Vianey-Liaud 1997; Emery 2004; Emery et al. 2007)

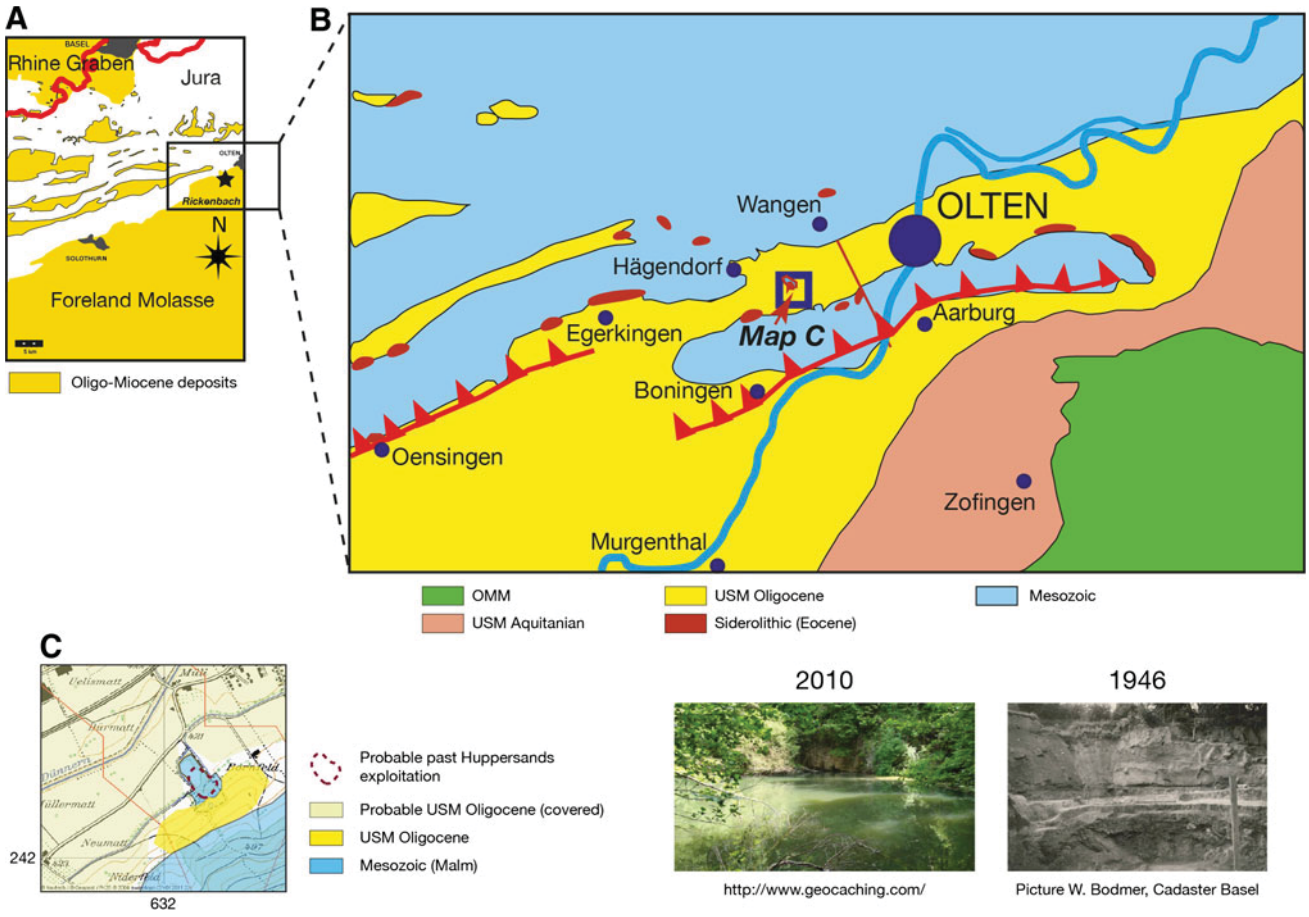


Fig. 1 Geographical and geological location of Rickenbach (late Chattian, Switzerland). **a** The Jura Molasse in Northwestern Switzerland (modified from Emery et al. 2007), **b** geology of the region of Olten (according to Mühlberg, 1915; Kehrer 1922; Erni and Kelterborn 1948; Jordi et al. 2003; Swisstopo, unpublished map), **c** detailed map of Rickenbach quarry. Pictures of the biotope taken in 2010, and of the old exploitation in 1946

very important amount of vertebrates, this time stored in the Naturmuseum Olten, was collected during this period by E. Fey and T. Schweizer, particularly.

Except for the carnivores (Helbing 1928) and for part of the rhinocerotid material (e.g., Heissig 1969; Michel 1983; Emery et al. 2007), most of the large mammals collected in Rickenbach remained undescribed. The small mammals were, however, intensively studied by Viret and Zapfe (1951; *Heterosorex*), Stehlin and Schaub (1951; rodents and insectivores), and Hrubesch (Hrubesch 1957; cricetids). Following the Congress of Paleogene in Bordeaux in 1962, Thaler (1965) published the first biostratigraphic scale based on European mammal levels for the Eocene and Oligocene. Rickenbach was considered for the first time in the international stratigraphic context as equivalent to the lower part of the Coderet level. Subsequently, diverse publications discussed the mammals from Rickenbach (e.g., Heissig 1969; Engesser 1975, 1982; Engesser et al. 1984), leading to the biozonation of Engesser and Mayo (1987). Since their publication in the "International Symposium on Mammalian Biostratigraphy and Palaeoecology" (Engesser and Mayo 1987), Rickenbach is definitively recognised as the European mammalian reference locality for level MP29. Remaining questions and arguments concerning the theridomorphs (e.g., Engesser and Mayo 1987; Vianey-Liaud and Schmidt Kittler 1987) were solved (e.g., Mödden 1993; Mödden and Vianey-Liaud 1997) and the eomyids were completely reviewed by Engesser (1990). In 1997, Engesser and Mödden published the official biozonation of the Swiss Molasse, confirming Rickenbach as the reference level for MP29. Detailed correlations between Swiss mammal levels and magnetostratigraphy were additionally published by Schlunegger et al. (1996), who clearly correlated the Rickenbach level (=MP29) within the chron 6 Cr, which actually corresponds to the interval 23.4–23.9 Ma (Fig. 1; Berger 2011).

To sum up, earlier literature and additional unpublished documents from the "Register of the Tertiary

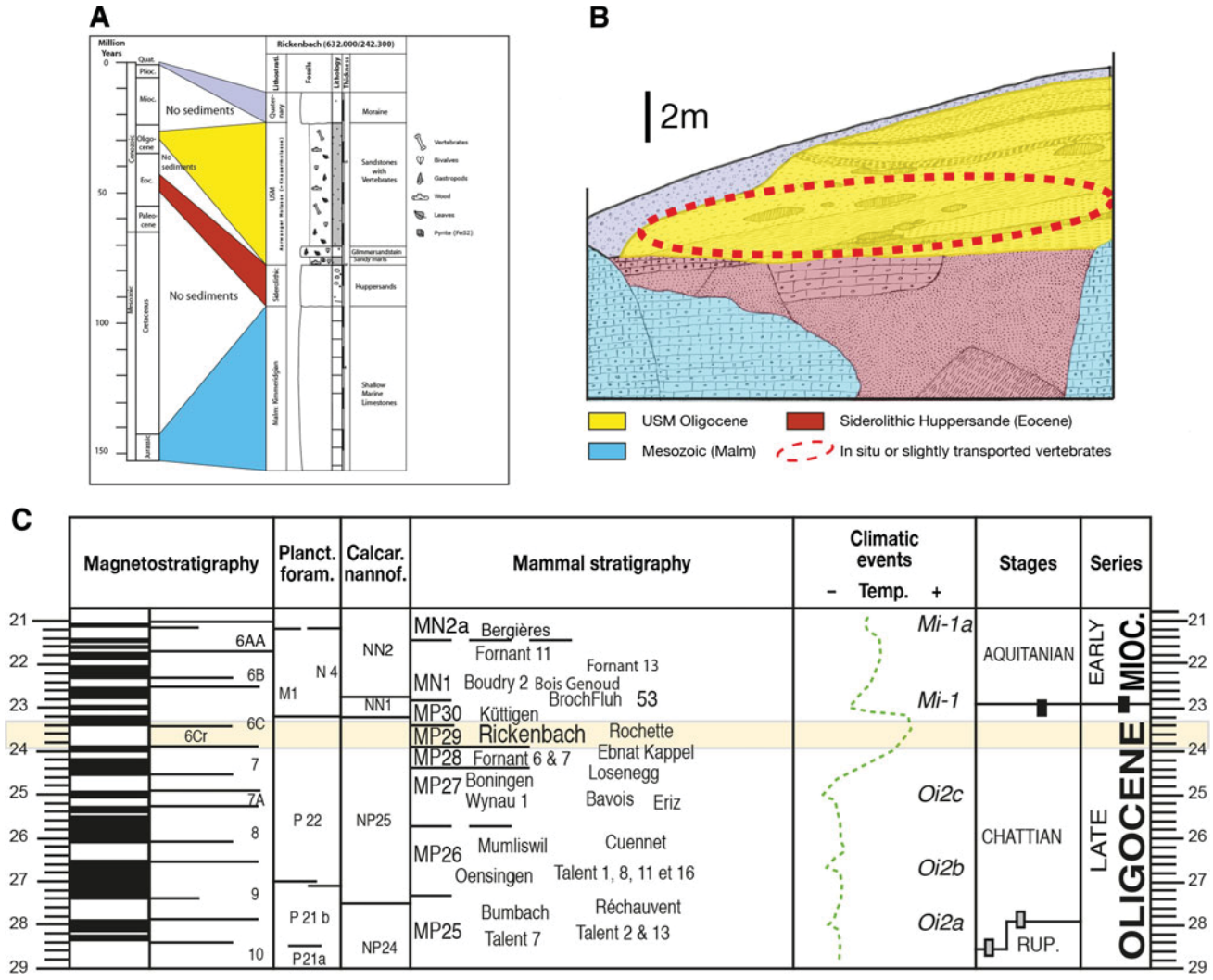


Fig. 2 Stratigraphic context of Rickenbach (late Chattian, Switzerland). **a** Sedimentological section (modified from Emery et al. 2007), **b** drawing of the deposits, modified from unpublished picture from D. Fey, 1935 (Naturmuseum Olten), **c** stratigraphic correlation of the Late Oligocene and earliest Miocene (modified from Berger 2011)

Mammal-Bearing Localities of the Naturhistorisches Museum Basel" show that: (1) the Molasse deposits above the Huppersands are composed of 4–8 m of alternating sands and sandy marls—with marly or micro-conglomeratic intercalations, representing a typical fluvial sedimentary pattern slightly discordant on the Jurassic limestone or the Eocene Huppersands; (2) no vertebrates were found in the Huppersands; (3) all vertebrates coming from these 4–8-m layers were geologically contemporaneous (Fig. 2). Therefore, Engesser and Mödden's statement (1997, p. 489) that "[…] in comparison with other reference faunas definitively obtained from one level, an origin of the mammal remains from layers slightly different in age cannot be excluded in the case of Rickenbach […]" should be updated. Indeed, even though a short post-mortem transport of the specimens is probable, no indication concerning a reworking was ever observed; neither in the geological and sedimentological context nor in the faunal diversity.

Material and methods

Palaeontology

The fossils discovered in Rickenbach are represented by many (>2,000) dental remains and isolated bones of terrestrial mammals. The specimens are housed in the Swiss institutions MHNG (Muséum d'histoire naturelle de Genève), NMB (Naturhistorisches Museum Basel), NMO (Naturmuseum Olten), and NMS (Naturhistorisches Museum Solothurn). Material for comparison is housed in UCBL-FSL (Université Claude Bernard, Faculté des Sciences de Lyon), MNHN

(Muséum national d'histoire naturelle de Paris), and USTL (Université des Sciences et Techniques du Languedoc, Montpellier). The descriptions, measurements, and diagnostic characters follow Scherler et al. (2011) for tapirids, and Heissig (1969), Guérin (1980), Antoine (2002), and Antoine et al. (2010) for rhinocerotids. Lihoreau (2003) and Boisserie et al. (2010) determined the methodology for bunodont cetartiodactyls (anthracotheres and suoids), and the terminology and biometry for ruminants follow Bärmann and Rössner (2011) and Köhler (1993). The taxonomic identifications of the rhinocerotids and ruminants include postcranial elements, but those of the tapirids and bunodont cetartiodactyls are exclusively based on dental remains. Biometrical dimensions are expressed in millimetres (mm) and the measurements of teeth are indicated by L × W. Body weights are expressed in grams (g).

Palaeoecology

We applied the cenogram method following Legendre (1989) to the mammal community of Rickenbach based on the terrestrial non-flying herbivores (in this study: Marsupialia, Lipotyphla, Glires, Rodentia, Perissodactyla, Cetartiodactyla). Table 2 lists the fauna of Rickenbach and the estimated body weights for each species used.

Body weights for perissodactyls and cetartiodactyls were evaluated using the regression of body mass (Legendre 1989) on the occlusal areas of m1s (L × W measurements). Body weights of mammals other than ungulates were taken from Legendre's data (1989). Furthermore, we compared our results with the contemporaneous fossil-community cenogram of La Milloque (MP29, France) and with five extant community cenograms (established by Legendre 1989) in order to qualitatively

Table 2 Estimated body weights of the herbivore terrestrial mammals sensu lato from Rickenbach (type locality MP29, Switzerland) and La Milloque (MP29+, France)

Fauna from Rickenbach	Body weight estimate (g)	Fauna from La Milloque	Body weight estimate (g)
Ronzotherium romani	1,790,000	*Anthracotherium magnum*	1,400,000
Anthracotherium magnum	1,420,000	*Diaceratherium lamilloquense*	1,040,000
Diaceratherium lamilloquense	1,040,000	*Doliochoerus quercyi*	48,000
Protapirus sp.	43,000	*Protapirus aginensis*	43,000
Microbunodon minimum	40,000	*Microbunodon minimum*	40,000
Palaeochoerus pusillus	22,000	*Bedenomeryx milloquensis*	32,000
Dremotherium guthi	20,000	*Palaeochoerus gergovianus*	31,000
Babameryx engesseri gen. et sp. nov.	16,000	*Dremotherium guthi*	18,000
"Amphitragulus" feningrei	13,000	*"Amphitragulus" quercyi*	8,000
"Amphitragulus" quercyi	8,000	*Amphilagus* sp.	2,700
Steneofiber dehmi	7,500	*Piezodus* sp.	1,800
Cainotherium sp. 2	2,500	*Cainotherium commune*	1,300
Archaeomys helveticus	1,000	*Archaeomys laurillardi*	1,050
Cainotherium sp. 1	700	*Melissiodon quercyi*	100
Archaeomys arvenensis	500	*Issiodoromys pseudanoema*	90
Amphechinus sp.	450	Lipotyphla sp.	70
Rhizospalax poirrieri	180	Marsupialia sp.	50
Melissiodon cf. *quercyi*	140	*Plesiosminthus schaubi*	40
Issiodoromys pseudanoema	125	*Eucricetodon praecursor*	30
Sciurus sp.	35	Lipotyphla sp.	22
Eucricetodon cf. *dubius*	30	*Pseudodryomys* sp.	21
Eucricetodon praecursor	25	*Adelomyarion vireti*	17
Amphiperatherium exile	21	Marsupialia sp.	16
Talpid indet.	20	*Eomys* sp.	15
Eomys cf. *ebnatensis*	20	*Glirudinus glirulus*	13
Eomys huerzeleri	20	*Pseudocricetodon* cf. *thaleri*	10
Adelomyarion vireti	18	*Rhodanomys* sp.	7
Dinosorex huerzeleri	15	*Peridyromys murinus*	7
Plesiosminthus promyarion	11	*Pseudotherydomys* sp.	6
Gliravus sp.	10		
Microdyromys cf. *praemurinus*	5		

The faunal lists have been modified from Brunet et al. (1981) and Engesser and Mödden (1997)

estimate the structure of the mammalian community in Rickenbach. The faunal list of La Milloque (Brunet et al. 1981) has been adapted with our personal observations, and the body weights of ungulates were re-evaluated. Relationships between extant community cenograms and the main environmental characteristics are based on Gingerich (1989), Legendre (1989), Rodriguez (1999), and Costeur and Legendre (2008). The slopes and gaps formed by three size classes (less than 500 g, more than 500 g but less than 250,000 g, and more than 250,000 g) give information on vegetation structure, annual precipitation, and temperature (Legendre 1989; Rodriguez 1999; Costeur and Legendre 2008). Comparing the shape of fossil-community structures with extant ones gives additional information on palaeoenvironments.

The ecomorphologic analysis of the ruminants is based on the morphology of the metapods and phalanges according to Köhler (1993). In the present study, the subdivisions of the habitats are simplified to two types: wooded (type A) and open (type B). Type A can be additionally divided into two: moderately humid (subtype A1) and very humid (subtype A2). The characterization of the palaeobiologic parameters of rhinocerotids mainly follows Becker et al. (2009), in order to define the anatomical types and the related environments by analogies with extant representatives. Body sizes are estimated by comparing the length of the metapods with the shoulder height of extant rhinoceroses. The estimated body weights are based on Legendre's aforementioned method and the regression of body mass on skull length (occipital condyles-premaxilla). Locomotion types (cursorial, mediportal, graviportal) are defined from the slenderness of the central metapods following the method of the GI (sensu Guérin 1980: TD diaphysis/L). The diets are evaluated by observing the occlusal patterns of the back teeth and by calculating the HI on the m3s (sensu Janis 1988: H/W). The feeding behaviour, or posture (head-holding down, intermediate, or up), is characterised from skulls by using the occipital side inclination and the angle of the occipital crest in lateral view (Bales 1996).

Systematic palaeontology

Order Perissodactyla Owen, 1848
Family Tapiridae Gray, 1821
Genus *Protapirus* Filhol, 1877
Protapirus sp.

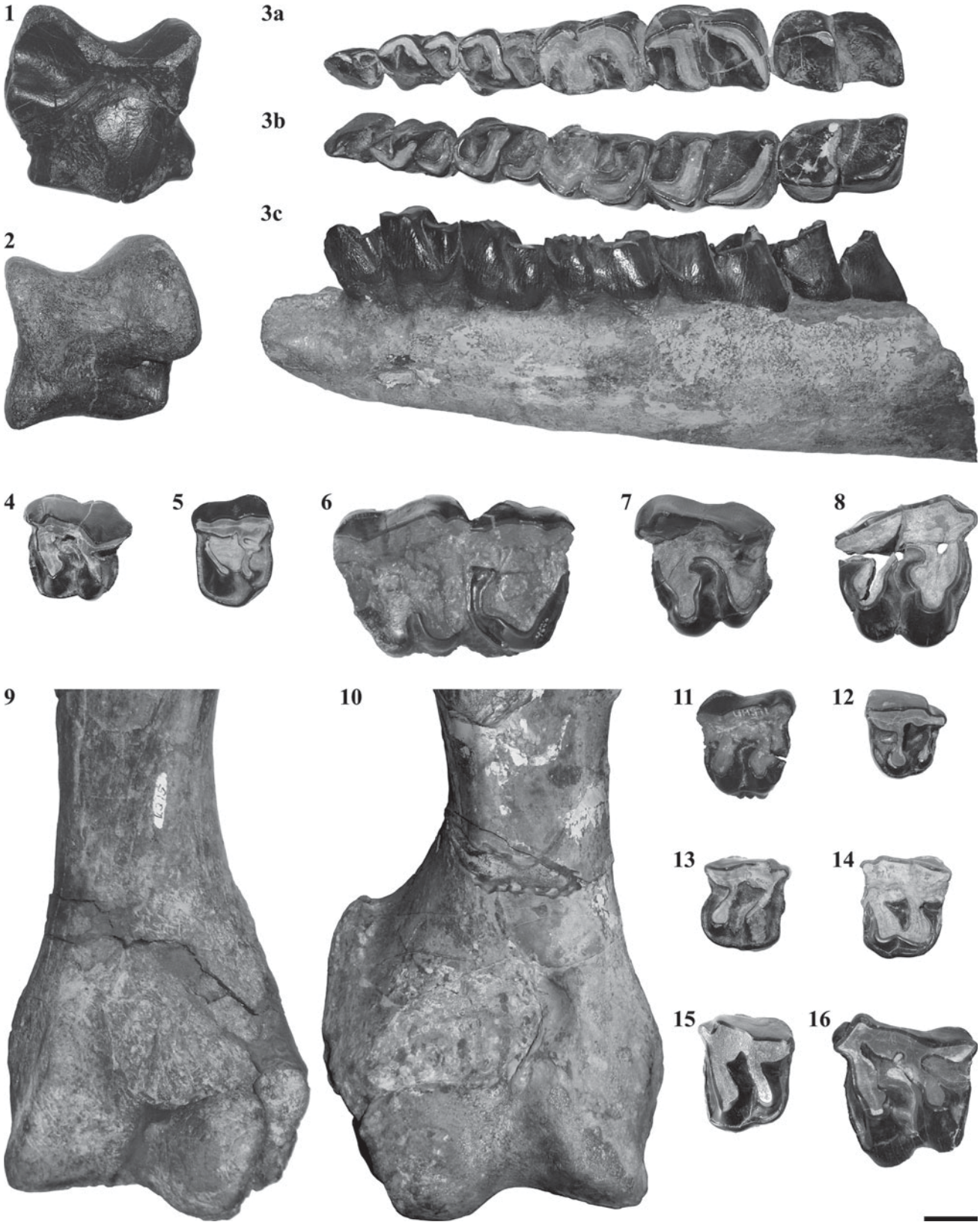
A unique fragmentary left m2 of *Protapirus* sp. (NMO-H10/64) has been discovered in the large amount of mammalian remains. It lacks its mesiolabial part, but its dimensions (18.5 × 11.0) and the presence of two vertical crests on the posterior side of the protolophid correspond to a Chattian species of the genus *Protapirus*. It is nevertheless not possible to discriminate between the two representatives of the Late Oligocene *P. bavaricus* (Oettingen-Spielberg, 1952) and *P. aginensis* (Richard, 1938).

Fig. 3 Latest Oligocene rhinocerotids of Rickenbach (type locality MP29, Switzerland). *Ronzotherium romani*: **1** left astragalus (NMO-K3/9), posterior view; **2** left astragalus (NMO-I12/20), anterior view; **3** sub-complete mandible (NMB-UM3832): right tooth row, occlusal view (**a**), left tooth row, occlusal view (**b**), left hemi-mandible, lateral view (**c**); **4** left D3 (NMO-I11/85), occlusal view; **5** left P3 (NMB-Ri24), occlusal view; **6** right P4-M1 (NMB-UM1840), occlusal view; **7** left M1 (NMO-I12/24), occlusal view; **8** right M1 (NMO-I3/13), occlusal view; **9** distal fragment of left humerus (NMO-K3/5), anterior view. *Diaceratherium lamilloquense*: **10** distal part of right humerus (NMB-UM973), anterior view; **11** right D4 (NMB-UM971), occlusal view; **12** right P2 (NMO-I1/104), occlusal view; **13** right P3 (NMO-I12/23), occlusal view; **14** left P3 (NMO-I11/73), occlusal view; **15** left P4 (NMB-HR1), occlusal view; **16** left M2 (NMB-Ri27), occlusal view. *Scale bar* equals 20 mm

Family Rhinocerotidae Gray, 1821
Subfamily Elasmotheriinae Bonaparte, 1845
Genus *Ronzotherium* Aymard, 1854
Ronzotherium romani Kretzoi, 1940
Figs. 3 and 4

The middle-sized, slender, and hornless rhinocerotid *Ronzotherium romani* is documented by 35 dental and postcranial remains. The most characteristic ones are a left I2 (NMB-UM6319), a fragmentary right i2 (NMB-UM807), a left D3 (NMO-I11/85), a left d1 (NMB-UM2574), a left P3 (NMB-Ri24), a fragmentary right maxilla P4-M1 (NMB-UM1840), two M1s (NMO-I12/24, NMO-I3/13), two fragmentary mandibles (NMB-UM3832, NMS-7707), a distal fragment of a left humerus (NMO-K3/5), a distal fragment of a right McIII (NMB-UM2570), two astragali (NMO-I12/20, NMO-K3/9), two right MtIIIs (NMO-K3/13, NMO-H9/9), and a right MtIV (NMO-I10/103).

According to Heissig (1969) and Brunet (1979), the specimens in question show dimensions and a combination of characters that are typical for *Ronzotherium*: the sections of I2 and i2 are almond shaped and oval, respectively. The cheek teeth are brachyodont with a strong lingual cingulum notched at the level of the medisinus, which joins the anterior and posterior ones. The ectoloph profile is somewhat waved with a smooth paracone fold, and weak mesostyle and metacone fold. The crochet and the antecrochet are usually absent on upper premolars, but there is a wide and deep postfossette. The upper molars bear a strong antecrochet and a straight posterior part of the ectoloph profile. The trigonid of the lower molars is angular and forms a right dihedron in occlusal view. The lingual opening of the posterior valley is U-shaped, and the hypolophid is transversely oriented.



The D3 and D4 bear a marked paracone fold, well-developed parastyle and metastyle, and reduced lingual and labial cingula. Furthermore, the base of the corpus mandibulae is straight; the mandible has a weak incisura vasorum, a weakly developed angulus mandibulae, and a subvertical ramus.

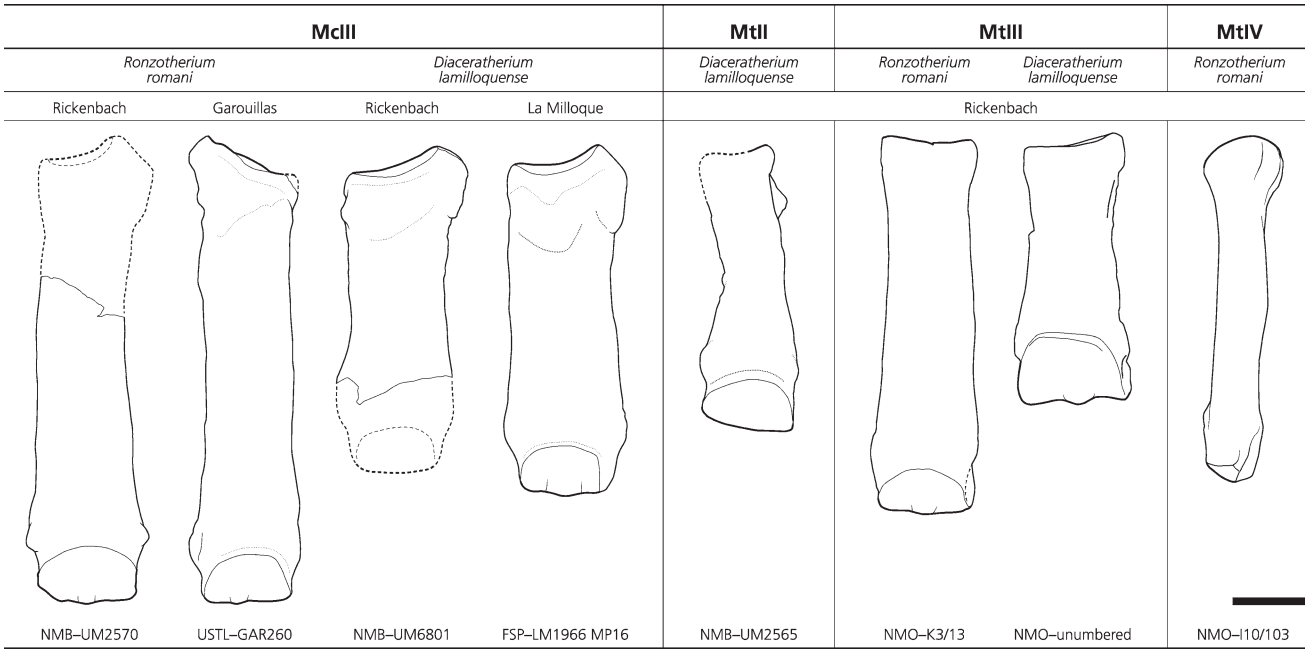


Fig. 4 Metapods (McIII, MtII, MtIII, and MtIV) of *Ronzotherium romani* and *Diaceratherium lamilloquense* from Rickenbach (type locality MP29, Switzerland) compared to the McIII of *R. romani* from Le Garouillas (MP25, France; de Bonis and Brunet 1995) and to the McIII of *D. lamilloquense* from La Milloque (MP29+, France; Michel 1983). *Scale bar* equals 30 mm

From the referred humerus (TD distal extremity = 113.0; minimal TD diaphysis = 60.0), the median constriction of the trochlea is somewhat deep ("diabolo-shape" sensu Antoine 2002). The two referred astragali are broader than high (mean of TD/H = 1.08) and shallow (APD/H = 0.56). The fibular facet is sub-vertical and transversally flat, and the collum tali is high. The postero-proximal border of the trochlea is nearly straight, and the trochlea itself is very oblique in respect to the distal articulation. The lateral lip is prominent. The calcaneal facet 1 is concave and its laterodistal expansion is present, rather low and broad. Facet 2 is flat and higher than wide, and facet 3 is small and unconnected to facet 2. The documented metapods are slender (mean GI on MtIII = 0.236), with a shorter MtIV (L = 137.0) compared to the MtIII (mean L = 156.5). The insertions for the interossei muscles are long and marked down to the distal half of the shaft. The intermediate reliefs are usually high and acute, and the proximal border of the anterior side of MtIII is concave. There are two flat and well-developed MtII-facets on the medial side of the MtIII; the MtIV has independent facets and is lacking the cuboid facet on the lateral side. There is no distal widening of the diaphysis of the MtIII.

The specimens from Rickenbach differ from the primitive ronzotheres *R. velaunum* (Aymard, 1853) and *R. filholi* (Osborn, 1900) by a general reduction of the cingula on the cheek teeth, a more advanced molarisation and a weaker crista on upper premolars, and a weak paracone fold and constricted protocone on upper molars. P2 is molariform (sensu Heissig 1969) with joined protoloph and ectoloph that are curved posterolingually, and straight metaloph. P3 and P4 (P3 mean = 32.25 × 40.75; P4 mean = 39.0 × 50.5) are semi-molariform (sensu Heissig 1969) with a posterolingually curved protoloph, longer than the roughly S-shaped metaloph. The referred M1s (mean = 51.0 × 56.5) are characterised by the absence (or strong reduction) of labial and lingual cingula, and by the presence of a constricted protocone. D3 and D4 (D3 = 40.0 × 41.0; D4 mean = 44.0 × 46.75) exhibit a quadrangular occlusal shape, weak parastyle and metastyle, as well as straight and posterolingually oblique protoloph and metaloph. d1 (14.5 × 7.5) is one-rooted and it bears a wide postfossettid. Regarding the mandible, the posterior border of the symphysis reaches the middle of p3 and the foramen mentale is located below the level of p2–p3. Additionally, the lower premolar series is short with respect to the molar series (mean Lp3–4/Lm1–3 = 0.45), the probable absence of p1/d1 in adults (no corresponding alveoli are attested on the referred mandible), the reduction of p2 (curved paralophid without constriction, reduced paraconid, and closed posterior valley), the strongly reduced lingual and labial cingulids, and the developed external groove of the lower cheek teeth, impede referring the large rhino from Rickenbach to *R. filholi* or *R. velaunum*. Most morphological features aforementioned are consistent with those of *R. romani* (e.g., Heissig 1969; Brunet 1979; Becker 2009;

Ménouret and Guérin 2009), however, being even more similar to the latest representatives of the concerned species, known from the latest Oligocene, as suggested by Brunet (1979) and Brunet et al. (1987).

Subfamily Rhinocerotinae Gray, 1821
Genus *Diaceratherium* Dietrich, 1931
Diaceratherium lamilloquense Michel, 1983
Figs. 3 and 4

The small-sized and mediportal–graviportal diacerathere *Diaceratherium lamilloquense* Michel, 1983 is documented by relatively few remains: nine isolated teeth (fragmentary left i2, NMB-Ri22; right D4, NMB-UM971; right P2, NMO-I1/104; left P3, NMO-I11/73; right P3, NMO-I12/23; left P4, NMB-HR1; left M2, NMB-Ri27; left m2, NMO-I11/75; right m2, NMO-I1/93), right humerus (NMB-UM973), and three metapods (fragmentary left McIII, NMB-UM6801; left MtII, NMB-UM2565; left MtIII, NMO-unnumbered).

According to Heissig (1969), Brunet (1979), and Ménouret and Guérin (2009), the available specimens show some similarities with those attributed to *Ronzotherium romani* (Kretzoi 1940), such as a continuous lingual cingulum joined to the anterior and posterior ones, a reduced labial cingulum, a distinct crista, and a wide postfossette on upper premolars. On P2, the protocone is less developed than the hypocone, and the M2s bear a strong antecrochet, as well as a simple crochet, and a crista. The metapods have sharp intermediate reliefs and distinct MtIV facets on MtIII. However, most specimens from Rickenbach are smaller in size than those of *Ronzotherium romani*, and they further differ morphologically from the latter by having a triangular i2 in cross section, a stronger reduction of the labial cingulum, a smooth ectoloph profile with a developed paracone fold, and an onset of the crochet on upper premolars, which are molariform (sensu Heissig 1969: separated protocone and hypocone). The protoloph is interrupted on P2 (30.0 × 30.0), with nearly transverse and straight protoloph and metaloph, and straight and posterolingually oblique protoloph and metaloph on P3 and P4, with a slightly constricted protocone and an onset of crochet and antecrochet on the latter (P3 mean = 32.8 × 40.3; P4 = 38.0 × 49.5). The referred M2 (54.0 × 58.0) shows a concave posterior part of the ectoloph profile. The lingual and labial cingulids on m2s (mean = 45.5 × 27.5) are strongly reduced, with a well-marked external groove and a developed, somewhat constricted, entoconid. D4 (37.0 × 38.0) displays a stronger reduction of the cingula, a narrow postfossette, short parastyle and metastyle, and a marked anterior groove on the protocone. The metapods are stockier (GI on MtIII = 0.329) with short insertions for the interossei muscles that are restricted to the proximal half of the shaft. In anterior view, the magnum facet on McIII is visible and the MtIII displays a concave proximal border and a distal widening of the shaft. There are no MtII facets on the MtIII, and vice versa. The referred humerus (L = 404.0; TD distal extremity = 128.0; minimal TD diaphysis = 58.0) displays a shallow median constriction ("egg-cup shape" sensu Antoine 2002).

Most of these features recall those of the early teleoceratine diaceratheres from the Late Oligocene of Western Europe (e.g., Michel 1983; Brunet et al. 1987; Ménouret and Guérin 2009). The dimensions mainly match those of the smallest representative of the latest Oligocene diaceratheres of Europe, *D. lamilloquense* (MP29; Michel 1983; Brunet et al. 1987). The referred humerus only is around 15% larger than the humerus from the specimen of La Milloque (NMB-LM1161) and it has similar size and proportions to that of *Diaceratherium massiliae* (UCBL-FSL-9523; Ménouret and Guérin 2009, Fig. 10.A). This may reveal wide metrical discrepancies within *D. lamilloquense* as noted in most of teleoceratines (e.g., Cerdeño 1993; Antoine 2002). Furthermore, the junior synonymy of *D. massiliae* Ménouret and Guérin 2009 with *D. lamilloquense* Michel 1983 could be questionable. Based on these observations, the concerned specimens, of which some have been misidentified as *R. romani* Kretzoi 1940 in former papers (e.g., left P4, NMB-HR1; Heissig 1969; Michel 1983; Becker 2003), are tentatively assigned to *D. lamilloquense*. A direct observation of the lost specimen of the NMB—fragmentary maxilla with M2–M3 illustrated by Michel (1983, pl. 8.f), coll. Heizmann—should support this assignation by showing a clearly concave posterior part of the ectoloph profile on M2 and fused ectoloph and metaloph on M3.

Order Cetartiodactyla Montgelard et al., 1997
Family Anthracotheriidae Leidy, 1869
Subfamily Anthracotheriinae Leidy, 1869
Genus *Anthracotherium* Cuvier, 1822
Anthracotherium magnum de Blainville, 1839–1864
Fig. 5

A complete review of the Swiss anthracotheres was recently presented by Scherler (2011). Dental remains (around 60) of the very large *Anthracotherium magnum* were discovered, represented almost only by isolated lower and upper teeth, along with a fragmentary left mandible (NMB-HR3). The canines (e.g., NMO-I12/35, NMO-I12/39) are large with a rounded section (mean = 36.5 × 31.0). The P2s (e.g., NMB-UM949, NMO-K2/27) and P3s (e.g., NMO-K2/29, NMO-K5/50) are sub-triangular without a real protocone, and their undifferentiated postparacrista and postmetacrista join the metastyle (P2 mean = 34.0 × 22.0; P3 mean = 36.5 × 28.0). Additionally, there is an accessory cusp on the distolingual side of the P3s. The P4s (e.g., NMB-UM948) are sub-rectangular with a

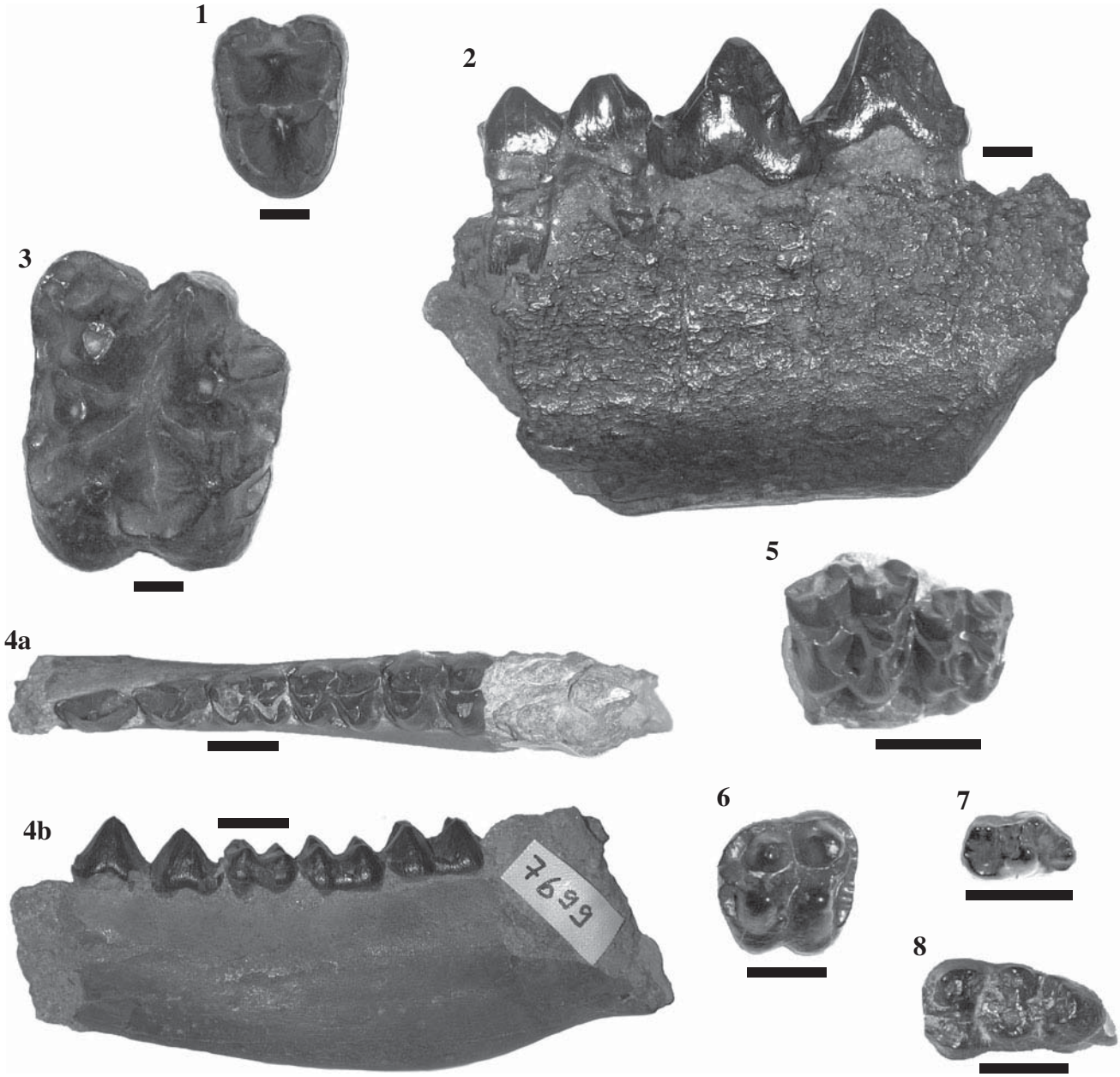


Fig. 5 Latest Oligocene anthracotheres and suoids of Rickenbach (type locality MP29, Switzerland). *Anthracotherium magnum*: **1** right P4 (NMB-UM948), occlusal view; **2** fragmentary left mandible with p3-m1 (NMB-HR3), lingual view; **3** right M3 (NMB-HR188), occlusal view. *Microbunodon minimum*: **4** fragmentary left mandible with p3-m3 (NMS-7699), occlusal (**a**) and labial (**b**) views; **5** right M1–M2 (NMO-I8/83), occlusal view. *Palaeochoerus pusillus*: **6** right M2 (NMB-UM1330), occlusal view; **7** left p4 (NMB-HR2590), occlusal view; **8** left m3 (NMB-Ri63), occlusal view. *Scale bars* equal 10 mm

well-developed cingulum almost all around the tooth (mean = 29.5 × 38.0). The trapezoidal upper molars (e.g., NMB-HR240, NMB-HR141, NMB-HR188) display a strong and oblique parastyle, and a metastyle shifted posteriorly. There is a mesiostyle, which is characteristic of the genus diagnosis (e.g., Lihoreau 2003), and a medium distostyle. Furthermore, the postprotocrista is isolated and distally directed, and does not join the premetacristule (M1 mean = 32.5 × 33.5; M2 = 52.5 × 59.0; M3 mean = 56.0 × 68.0). The p4s (e.g., NMB-HR3) are inscribed in a right-angled triangle, without any mesiostylid or distostylid, and their endoprotocristid is well developed and distolingually directed. Furthermore, there is a short lingual accessory cristid initiating from the preprotocristid and distally directed (33.5 × 21.5). The sub-rectangular m1s (e.g., NMB-HR3, NMB-HR144) and m2s (e.g., NMB-HR3) bear four bunodont cuspids with slightly developed mesial and distal cingulids. The prehypocristid is

mesiolingually directed and joins the distal wall of the postmetacristid, forming a large accretion in the middle of the sagittal valley (m1 mean = 37.0 × 28.0). The unique m3 (NMB-HR3) bears an additional talonid that shows a distinct entoconulid well separated from the hypoconulid. Along with the large size of the specimens (e.g., NMB-UM3184, left M3 = 56.5 × 68.5), these two latter features are diagnostic of *Anthracotherium magnum* de Blainville 1839–1864 (Scherler 2011).

Subfamily Microbunodontinae Lihoreau and Ducrocq, 2007

Genus *Microbunodon* Depéret, 1908

Microbunodon minimum (Cuvier, 1822)

Fig. 5

The small anthracothere *Microbunodon minimum* (Cuvier, 1822) is also mainly represented in Rickenbach by dental remains (around 90). It comprises many fragmentary maxillae (e.g., NMO-H11/98, NMO-K5/29, NMB-Ri1) and mandibles (e.g., NMB-Ri60, NMO-H11/30, NMO-I12/9) with upper and lower tooth rows, as well as isolated teeth. The canines (e.g., NMB-Ri56) are transversally compressed with mesial and distal careens, and they show sexual dimorphism marked by blade-like C in males (12.0 × 7.0). The molars are bunoselenodont. On the upper molars (e.g., NMO-H10/70, NMB-HR145), the parastyle is strong and sub-vertical, and the mesostyle is V-shaped (M1 mean = 12.0 × 13.5). There is a well-developed distostyle, but no mesiostyle. The labial cuspids of the lower molars are crescent-like compared to the lingual ones, which are more conical (m1 mean = 12.0 × 8.5; m2 mean = 14.0 × 10.5; m3 mean = 24.5 × 11.0). The m1s (e.g., NMB-UM1329, NMO-H10/92) and m2s (e.g., NMO-K9/100, NMS-7715, NMS-7709) are sub-rectangular, with short mesial and distal cingulids. Furthermore, the talonid of the m3s (e.g., NMB-HR146, NMO-K10/241) bears a single cuspid, the hypoconulid, which forms a loop-like hypolophid.

Superfamily Suoidea Gray, 1821

Family Palaeochoeriidae Matthew, 1924

Genus *Palaeochoerus* Pomel, 1847

Palaeochoerus pusillus Ginsburg, 1974

Fig. 5

The teeth of suoids from Rickenbach (around 20, see Scherler 2011) are referred to the small palaeochoerid species *Palaeochoerus pusillus*. The upper molars (e.g., NMB-UM1330, NMB-UM2588, NMO-K5/11) are bunodont and simple, with four main cuspids that are well conical. They do not display any accessory cuspids. The mesial, distal, and labial cingula are strong, but there is no lingual cingulum. There is a weak entostyle and the distostyle is well developed (M1 = 12.5 × 11.0; M2 = 12.5 × 13.0; M3 = 13.0 × 13.5). The p4s (NMB-UM2590, NMB-HR242) bear a lingual metaconid well differentiated from the protoconid. The hypoconid is less developed, and there is no entoconid. The mesio- and distostylids are slightly developed (p4 mean = 11.25 × 6.75). The lower molars (e.g., NMB-Ri64, NMO-H10/74, NMO-K9/105) are simple bunodont teeth that only display a metaconulid as an accessory cuspid. There is a short and weak mesial cingulid, but no real stylids. The transverse valley is wide and continuous, as is the sagittal valley that separates the first lobe from the second (m2 mean = 12.0 × 8.5; m3 mean = 21.0 × 11.5). In comparison to *Doliochoerus quercyi* from La Milloque, the specimens from Rickenbach differ by the absence of any accessory cuspids on the upper molars, the absence of a real paraconid, and the absence of a prehypoconulid on the m3s. Indeed, the talonid of the m3s from Rickenbach is simple, without any accessory cuspid between the second lobe and the hypoconulid. This latter feature is characteristic of the species *Palaeochoerus pusillus*. Additionally, the specimens from Rickenbach display an intermediate size between the very small species *Palaeochoerus paronae* and the larger *P. gergovianus* and *P. typus*. These latter species display accessory cuspids on their upper molars that are not present on the specimens from Rickenbach. Further comparisons to the holotype of *P. pusillus* (MNHP-Qu15, Phosphorites du Quercy) figured by Hellmund (1992) confirm the assignment of the specimens from Rickenbach to *Palaeochoerus pusillus* Ginsburg, 1974.

Suborder Ruminantia Scopoli, 1777

Infraorder Pecora Flower, 1883

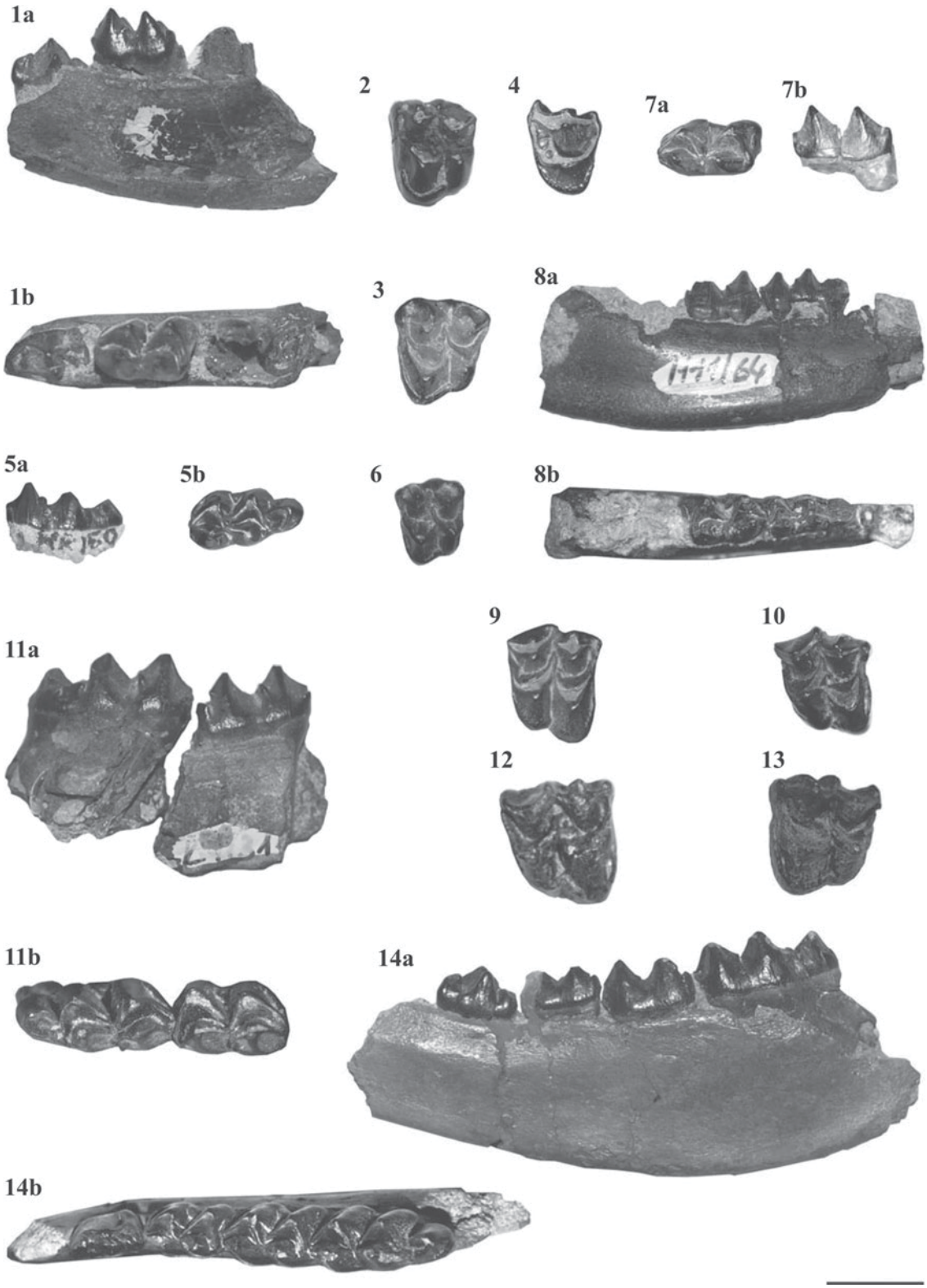
The ruminants are currently reviewed by B. Mennecart in the frame of his PhD thesis. Latest Oligocene and Early Miocene familial attributions are mainly speculative and confusing, and will not be proposed for this article. All the ruminants collected in Rickenbach were initially stored under the name *Amphitragulus* sp.

Genus *Dremotherium* Saint-Hilaire, 1833

Dremotherium guthi Jehenne, 1987

Figs. 6 and 7

Dremotherium guthi is the most represented ruminant in Rickenbach with more than 50 remains. The material includes isolated upper teeth (e.g., NMB-UM2594, NMB-UM1331, NMO-L6/38), lower jaws (e.g., NMB-HR9, NMB-UM2595), and postcranial remains. The dental features are characteristic to *Dremotherium*. Indeed, these teeth are larger and more advanced in comparison to those of ruminants from the latest Oligocene (NMO-K4/31, m2 = 11.4 × 7.2, m3 = 15.5 × 7.0; NMO-I7/7, M2 = 11.4 × 12.8). The crowns are high and the cusps are well selenodont (NMB-HR162, NMO-L6/38). The quadratic



upper molars bear a well-developed metaconule (NMB-UM1331, NMO-I7/37). The postprotocrista is long and highly curved, and the premetaconulecrista is distally forked. The paracone rib displays an anterior groove, and the metacone rib, when present, is weak. The mesostyle is well developed and aligned with the premetacrista and the postparacrista. The metastyle forms a small column and the entostyle is weak or absent. There is no lingual cingulum at

◄ **Fig. 6** Latest Oligocene ruminants of Rickenbach (type locality MP29, Switzerland). *Babameryx engesseri* gen. et sp. nov.: **1** right fragmentary mandible (NMO-K5/7) with erupting p4 and m1, lingual (**a**) and occlusal (**b**) views; **2** Holotype: left M1 (NMO-K11/15), occlusal view; **3** left M3 (NMB-UM2833), occlusal view; **4** right P4 (NMB-UM793), occlusal view. "*Amphitragulus*" *quercyi*: **5** right m3 (NMB-HR150), lingual (**a**) and occlusal (**b**) views; **6**, left M1 (NMO-I9/48), occlusal view. "*Amphitragulus*" *feningrei*: **7** right m2 (NMB-UM796), lingual (**a**) and occlusal views (**b**); **8** left fragmentary mandible with d4-m1 (NMO-H11/64), lingual (**a**) and occlusal views (**b**); **9** right M1 (NMB-HR164), occlusal view; **10** right M3 (NMO-I7/4), occlusal view. *Dremotherium guthi*: **11** left m2–m3 (NMO-K4/31), lingual (**a**) and occlusal (**b**) views; **12** right M2 (NMO-I7/7), occlusal view; **13** left M2 (NMO-L6/38), occlusal view; **14** right mandible with p4-m3 (NMO-26578), lingual (**a**) and occlusal (**b**) views. *Scale bar* equals 10 mm

the level of the protocone. The total length of the lower molar row is smaller than those of *D. feignouxi* and similar to those of the paratype *D. guthi* (for Rickenbach, L m1–m3 = 35.0; for La Milloque, L m1–m3 = 37.0). The p4 is laterally compressed and its well-developed mesiolingual conid possesses an anterolingual cristid (NMB-HR9, NMB-UM2595). The lower molars have widely open trigonid and talonid due to slightly backward oriented internal postprotocristid and posthypocristid (NMB-UM1603, NMO-I7/31, NMO-I7/64). The lingual wall is flat with large cristids, and the metaconid and entoconid ribs are reduced. The postentocristid does not reach the large and globular entoconulid, and this forms a small gap between these two features. The metastylid is small and salient, and a small spur is present on the anterolingual part of the lower molars. The external postprotocristid is present and usually very well marked.

Postcranial remains have been assigned to *Dremotherium guthi* due to their very large size in comparison to the other ruminants present in Rickenbach (Hiard 2010). With its aligned trochlea, the astragalus (e.g., NMO-K2/48) is characteristic to Pecora. The metapodial bones (e.g., NMB-2836) are elongated with weakly developed and slightly dorsally flattened condyles. The extensor tendon forms a long groove on the proximal part of the bone. The proximal phalanx (e.g., NMO-K2/52) is robust with a flattened outline of the distal articulation. The outline of the dorsal surface is slightly concave, and the external side of the bone is straight. The middle phalanx is short and broad with a thinner distal part. The proximal articular facet is

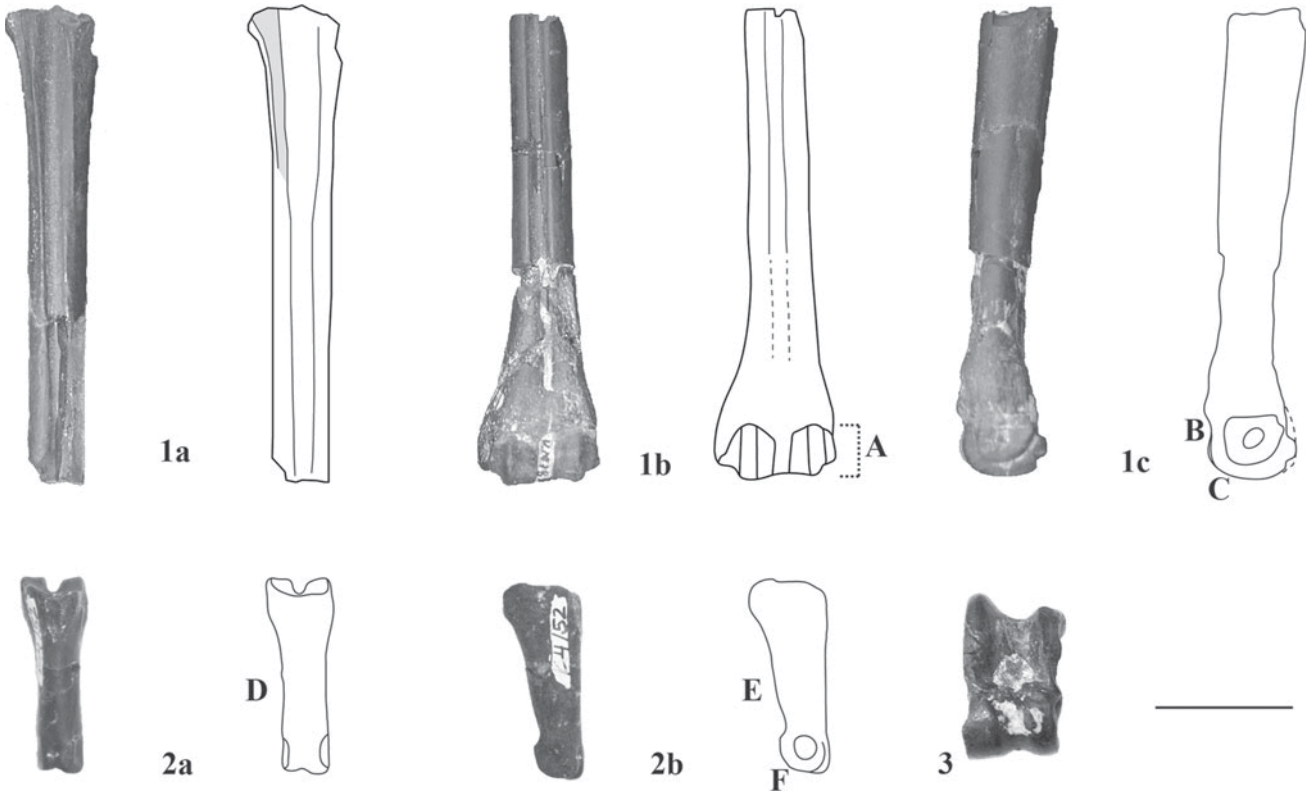


Fig. 7 Postcranial remains of *Dremotherium guthi* of Rickenbach (type locality MP29, Switzerland). **1** fragmentary right metatarsus (NMB-UM2836), proximal part in dorsal view (**a**), distal part in dorsal view (**b**), distal part in lateral view (**c**); **2** left proximal phalanx (NMO-R4/52), dorsal (**a**) and lateral (**b**) views; **3** right astragalus (NMO-R2/48), dorsal view (**3**). Light-grey area: long furrow for the lateral extensor tendon; *A* low articular surfaces with well-individualised condyles, *B* deep grooves, *C* flattened outline of the condyle, *D* straight outline of the external side, *E* straight outline of the palmar side in lateral view, *F* flattened dorsal articulation. *Scale bar* equals 20 mm

slightly concave. The distal articular facet is wide and triangular with a distally oriented tuberosity.

Genus *Amphitragulus* Croizet in Pomel, 1846

The review of the species of the genus *Amphitragulus* and their relationships with *Pomelomeryx* and *Dremotherium* are still unresolved (Jehenne 1985; Blondel 1997). Because the complete review is out of frame for the present contribution, we keep the name *Amphitragulus* for the species *quercyi* and *feningrei*, but with quotation marks.

"Amphitragulus" quercyi Filhol, 1887
Fig. 6

The smallest ruminant from Rickenbach, *"Amphitragulus" quercyi*, is very rare and seems to be only represented by dental remains (5 fossils). The teeth are bunoselenodont with a low crown. The upper molars possess a reduced external postprotocrista (NMO-I9/48) and a slightly reduced metaconule. The paracone rib is salient, but there is no metacone rib. The para-, meso-, and metastyles are salient. The lingual cingulum, when present, is very weak. The lingual wall of the lower molars shows highly bulged cuspids (NMB-HR150). The internal postprotocristid and the very short posthypocristid are transversal one to each other and form a small trigonid and talonid. The metaconid and the entoconid are aligned, and the metastylid forms a large small column. The external postprotocristid is deep, and the third basin is small and pinched. The specimens from Rickenbach are similar in shape and size (NMB-HR150, m3 = 11.9 × 6.0) from those described by Blondel (1997) in Pech Desse (mean dimensions for m3s = 12.0 × 5.8) and Pech du Fraysse (mean dimensions for m3s = 11.8 × 5.7), and from the holotype of *Amphitragulus quercyi* (MNHN-Qu4771, m3 = 11.3 × 5.3).

"Amphitragulus" feningrei Schlosser, 1925–1926
Fig. 6

Definitive and deciduous teeth (around 20) of the medium-sized ruminant "*Amphitragulus*" *feningrei* have been discovered. Their crowns are selenodont, but more brachyodont than those of *Dremotherium guthi* Jehenne, 1987. The upper molars are almost quadratic, slightly laterally compressed (NMB-HR164, NMO-I7/3, NMO-I7/4). The labial cusps are not aligned, and the metaconule is slightly reduced. The external postprotocrista is short and curved. The paracone is globular with a well-developed rib, but the metacone rib is absent. The para- and mesostyles are globular and form small columns, whereas the parastyle is anteriorly projected. There is no lingual cingulum. The lower molars possess small trigonid and talonid that form an acute angle (NMB-UM796, NMO-H11/64, NMO-K8/64). The lingual cuspids are sharp and laterally compressed, and their ribs are bulged. The entoconulid and metaconulid are both small, but the latter is more salient. Additionally, the external postprotocristid is very deep.

The holotype and paratypes of *Amphitragulus feningrei* Schlosser, 1925–1926 from Peublanc (MP30) stored in Munich had been lost or destroyed during World War II (G. Rössner and K. Heissig, pers. comm.). The figured specimens of Schlosser (1925–1926, Fig. 14) are similar in size and shape (excluding Fig. 14d, see *Babameryx engesseri* gen. et sp. nov. below) to those described and figured by Viret (1929, pl. 31, Figs. 13–14) from Coderet (MP30; UCBL-FSL-97.731: d4 = 9.7 × 4.0, m1 = 8.9 × 5.1) and to the specimens from Rickenbach (MP29; NMO-H11/64: d4 = 9.8 × 4.5, m1, 8.3 × 5.7). This species is clearly different from the other *Amphitragulus* species in having more selenodont crowns. Moreover, the cusps are sharp and the parastyle is globular and anteriorly projected, which seems to be unique amongst the Oligocene and Early Miocene ruminants. Therefore, this species should probably be assigned to a new genus (B. Mennecart, pers. obs.).

Genus *Babameryx* gen. nov.

Type species. *Babameryx engesseri*

Diagnosis. Medium-sized, brachyodont bunoselenodont Pecora; p4 compact and possessing well-formed mesolingual conid and anterior stylid; lower molar possessing highly bulged lingual cuspids without rib and a protoconid with an external postprotocristid; P4 stocky with a deep lingual cingulum and a central fold; upper molars with reduced metaconule, large and highly bulged paracone rib and metacone rib, and deep cingulum surrounding the protocone.

Etymology. From *Baba-*, "elder" or "patriarch" in eastern languages (Arabic, Russian, Slavic), and *-meryx*, Greek for "ruminants", in reference to the primitive features of this Eupecora.

Babameryx engesseri sp. nov.
Fig. 6
1914 v pars Ruminantia incertae sedis Stehlin: 185.
1987 v pars *Amphitragulus* sp. Engesser and Mayo: 76.
1997 v pars *Amphitragulus* sp. Engesser and Mödden: 488.
2007 v pars *Amphitragulus* sp. Emery et al.: 56, not fig. 10.

Holotype. NMO-K11/15, left M1 (8.9 × 10.7).

Paratype. NMO-K5/7, right fragmentary mandible with erupting p4 and m1 (8.2 × 4.2 and 9.3 × 6.4, respectively); NMB-UM2833, left M3 (10.0 × 11.6); NMB-UM793, right P4 (7.6 × 8.8).

Etymology. In tribute to our esteemed colleague and friend, Burkart Engesser, in recognition of his palaeontological investigations in the Swiss Molasse Basin, and especially in Rickenbach.

Stratum typicum. Sandstone bed of the Aarwanger Molasse of the USM (Lower Freshwater Molasse), European mammal reference level MP29.

Type locality. Rickenbach (NW Switzerland, Swiss coordinate grid: 632.200/242.300).

Occurrence. Latest Oligocene (MP28-30) from Germany (Gaimersheim 1) and Switzerland (Rickenbach, Küttigen).

Diagnosis. Only known species of the genus.

Nomenclatural remark. This new species must be referred to as *B. engesseri* Mennecart, 2011, following article 50.1 and the "recommendation 50A concerning multiple authors" of the International Code of Zoological Nomenclature (1999, 52, 182).

The scarce referred remains of a new medium-sized ruminant have been discovered in Rickenbach. The material includes upper and lower teeth that display extremely primitive and unique features amongst the Pecora from the Oligocene of Europe, with pretty bunodont and brachyodont crowns. The P4 is stocky (NMB-UM793), with salient and well-developed anterior style, posterior style, and central fold. A deep cingulum surrounds the lingual cone. The upper molars are triangular due to a reduced metaconule (NMB-UM791, NMB-793, NMB-3542, NMO-K11/15). The external postprotocrista is short and straight, and the paracone rib is large and highly bulged. The metacone is globular and highly bulged on the labial wall. The parastyle and mesostyle form globular small columns. A deep cingulum surrounds the protocone. The p4 is characteristic to Pecora in being compact and possessing a well-formed mesiolingual conid (NMO-K5/7). There are no postero- and anterolingual cristids, but there is an anterior stylid. The mesiolabial conid is high and well developed, forming a groove on its posterolabial part. The posterolingual conid is elongated. No cingulids can be observed. The lower molars possess a transverse labial cristid forming a small trigonid and a talonid (NMO-K5/7, NMO-K10/184). The postentocristid is very short, and the lingual cuspids are highly bulged and without rib, which gives a clear primitive aspect to the molars. However, the protoconid possesses an external postprotocrista. The metastylid is very weak; the ectostylid is weak when present; and the entoconulid, globular. Furthermore, the anterior cingulid is strong.

This species clearly differs from the older European pecoran genera *Gelocus* and *Prodremotherium* in having a deep external postprotocrista and a short and advanced p4. Moreover, the molars are highly bunodont; the metaconule and the external postprotocrista are reduced; a deep cingulum surrounds the protocone; and the lower molar lacks a metastylid. These primitive features clearly exclude an affiliation to the classical European Late Oligocene and Early Miocene genera *Amphitragulus*, *Dremotherium*, *Bedenomeryx*, *Andegameryx*, or *Oriomeryx*. The referred upper cheek teeth, however, could correspond to the destroyed upper dentition described as *Amphitragulus feningrei* by Schlosser (1925–1926, Fig. 14d). However, the holotype of *A. feningrei*, which is represented by a lower tooth row, is clearly different from this new species (see the above description of "*Amphitragulus*" *feningrei*). For these reasons, the referred specimens are assigned to *Babameryx engesseri* gen. et sp. nov. According to Mennecart (PhD thesis in progress), this new taxa was also recorded in the contemporaneous localities of Gaimersheim 1 (MP28) and Küttigen (MP30). *Babameryx engesseri* gen. et sp. nov., just like the genera *Dremotherium* and *Amphitragulus*, does not possess direct phylogenetic links with older European ruminants (B. Mennecart, pers. obs.). These mammals, along with the anthracotheriid *Microbunodon* (Lihoreau et al. 2004; Scherler 2011), probably came from a large Asiatic migration during MP28.

Palaeoecology

Diverse palaeoecologic proxies have been used on the fossils from Rickenbach in order to characterise the palaeoenvironment and palaeoclimate that prevailed in this region during the latest Oligocene. The results obtained from cenogram (Fig. 8) and ecomorphologic (Figs. 4, 7) studies are summarised here, and the interpretations of the habitat, based also on literature data, are discussed in this section.

Cenogram analysis

The mammalian community of Rickenbach comprises 31 terrestrial herbivorous and non-flying species (Table 2) and gives an interesting range of body sizes, which allowed us to establish a cenogram for this community (Fig. 8). According to Legendre (1987), Costeur (2005a) classically considered five size classes to compose the mammalian communities (body weights in grams: class 1 = 0–12.5, very small; class 2 = 12.5–500, small; class 3 = 500–8,000 or 10,000, medium; class 4 = 8,000 or 10,000–250,000, large; class 5 = above 250,000, very large). The cenogram of Rickenbach possesses two main breaks separating three different mammal groups. The very large mammals (class 5) from Rickenbach are relatively diversified with three species. The first break is due to the lack of large mammals (between 50,000 and 250,000 g, class 4). Although the medium (class 3), small (class 2), and very small (class 1) mammals form a homogeneous group that is highly diversified with 28 species, the second and smaller break occurs

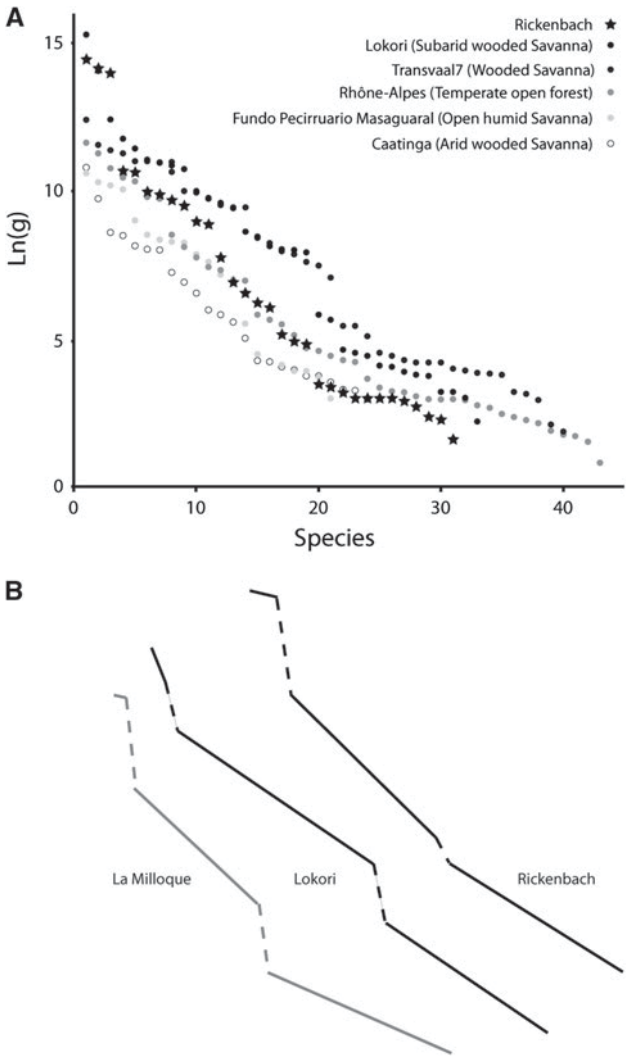


Fig. 8 Cenogram from Rickenbach (the body weights of each species are proposed in Table 1) compared with: **a** current savannah faunas (data from Legendre 1987, 1989); **b** La Milloque (France, latest Oligocene) and Lokori (Kenya, present), with schematic representation of cenograms showing two breaks each

between the small mammals (class 2) and the medium mammals (class 3). The first slope is additionally steeper than the second one.

The shape of the cenogram from Rickenbach is closely related to those of modern savannahs by the number of present mammals (Fig. 8). The habitat extrapolated from the mammalian community of Rickenbach is very similar to that of the wooded savannah of Lokori (Kenya) in the following points: very large mammals of class 5 (elephants and hippopotamuses), first break right after them, and second break. According to Rodriguez (1999), the fact that the second gap is smaller in Rickenbach than in Lokori could be due to a more wooded environment for the former. The similar number of small and very small mammals could indicate a similar warm climate (Legendre 1989). Lokori is dominated by dry conditions with seasonal rainfalls, but this 600 m high sub-arid savannah may be less dense than the environment of Rickenbach due to the presence of more abundant large mammals (Legendre 1987, 1989).

The structure of the community from Rickenbach is characteristic of those of the latest Oligocene in Europe (MP28-30). The cenograms established for the French localities (e.g., La Milloque, MP29+) possess also two breaks due to a lack of medium-sized species (class 3) and a high number of small mammals (Fig. 8; Legendre 1987, 1989; Costeur 2005b). Legendre (1989) and Costeur (2005a) interpreted this shape of cenogram as corresponding to a quite arid and open environment. However, Rickenbach possesses more medium mammals and a smaller second break, which may indicate a more wooded environment than in La Milloque. The number of small mammal species is greater than that reported from older Oligocene localities (such as St-Henri, St-André, St-Menoux, and Mas de Pauffié, MP26). In this aspect, Rickenbach may correspond to a warmer climate (Legendre 1987) probably linked to the Latest Oligocene Warming. However, Rodriguez (1999) demonstrated that the slope of the micromammals, which is correlated to the number of species, does not seem to be associated with temperature.

Ecomorphologic analysis

Ruminants

There are similar species of ruminant in Rickenbach and La Milloque (*Dremotherium guthi* and "*Amphitragulus*" *quercyi*). A microwear analysis on the mammals from La Milloque reveals that the smallest species fed mainly on leaves, whereas the largest were pure grazer (Novello et al. 2011). The appendicular skeleton of "*A.*" *quercyi* is similar to Cephalophini and animals of light forests (Blondel 1998).

The appendicular bones of *D. guthi* show a clear mixing of adaptations between the types determined by Köhler (1993) as wooded (type A) and open (type B) environments (Fig. 7). The metapods are elongated (type B) and become distally broader (type A). Deep grooves can be observed above the distal articular surface (type B). The distal articulation is low with dorsally flattened and well-individualised condyles (sub-type A1). The lateral view reveals that the outline above the articulation is dorsally convex and palmarly concave (type A). In the proximal part, the furrow for the lateral extensor tendon is long (type A). The proximal phalanges are robust (type A), with a flattened distal articulation on the palmar side (type B). External side is straight dorsally (type A), and the outline of the dorsal surface is slightly concave (type B). In lateral view, the

outline of the palmar side is straight (type B). The middle phalanges are short and broad (type A), but become distally thinner (type B). The proximal articular surface is laterally slightly concave (type A). The distal articulation shows a triangular outline from its internal view, with the angle distally directed (type A). Furthermore, the articular surface is extensive dorsally and palmarly (type B).

According to this description, *D. guthi* probably lived in a mixed habitat, such as wooded savannah, or a thin wooded area along a river. Additionally, it is most probable that *D. guthi* had a different ecology from *D. feignouxi*, a later species of the same genus. Indeed, *D. feignouxi* shows a characteristic morphology of type B, and probably lived in a more open area (Becker et al. 2010). Furthermore, *D. guthi* was a mixed feeder (Novello et al. 2011), whereas *D. feignouxi*, with its elongated cervical vertebrae, was a leaf-eater (Viret 1929; Janis and Scott 1987). *Dremotherium guthi* can be compared to the extant bovid *Tragelaphus angasii*, which has the same diet (Nowak 1999) and similar metapods in shape (but not in size). *T. angasii* lives on the edge of the forest by day and feeds in an open area by night (Nowak 1999), *D. guthi* may have a similar ecology. Such results confirm thus an environment ranging from light forest to more open areas for Rickenbach, such as suggested in La Milloque (Novello et al. 2011).

Rhinocerotids

The palaeoecologic parameters of *Ronzotherium romani* are close to those of *R. filholi* (mean L for McIII = 194.0; mean L for MtIII = 158.0; McIII GI = 0.212; MtIII GI = 0.222; Brunet 1979), even though the most recent representative of *R. romani*, in Rickenbach, is slightly less slender (mean L for McIII = 156.5; mean GI for MtIII = 0.236). Although the use of Legendre's method to estimate body weight is assumed for the cenogram construction to have a homogeneous data source, this method does not always seem adequate for the slender rhinocerotids (Becker et al. 2009), given an overestimation of body weights. By analogy with biometric data of extant rhinocerotids (Guérin 1980), *Ronzotherium romani* was probably of medium size, similar to *Diceros bicornis* (shoulder height of 1.6 m, Nowak 1999), and had a small body weight, similar to *Dicerorhinus sumatrensis* (800,000 g, Nowak 1999). In this regard and based on the regression of body mass on skull length (occipital condyle-premaxilla, Becker et al. 2009) of the specimen from Vendèze (MP24, France; Brunet 1979, Tab. 52), the body-weight estimate of *Ronzotherium romani* is 780,000 g. One should notice that this comment on the estimation of ronzothere weights does not affect the general interpretation of the cenogram established in this study. The GI calculated from the metapods is low (McIII GI = 0.192, USTL-GAR260 from Le Garouillas; de Bonis and Brunet 1995; MtIII GI = 0.236, NMO-K3/13 and NMO-H9/9 from Rickenbach), corresponding to a cursorial locomotion type that does not exist in modern rhinoceroses. The low hypsodonty index (HI = 1.0, NMB-UM3832 from Rickenbach) and the down head posture evaluated by analogy with the skulls from Villebramar (*R. filholi*, MP22, France; Brunet 1979, fig. 13, pl. 10) and Vendèze (*R. romani*, MP24, France; Brunet 1979, fig. 15, pl. 18) seem to indicate that *R. romani* was a regular browser, probably feeding preferentially on short vegetation (Janis 1988; Becker et al. 2009).

The estimated body weight of *Diaceratherium lamilloquense* (1,043,000 g) is based on the m1 measurements of the holotype from La Milloque (Michel 1983, tab. 8). It corresponds to a small-to-medium body weight similar to *Diceros bicornis* (1,200,000 g, Nowak 1999). By comparing the MtIII lengths of the specimen from Rickenbach (MtIII L = 112.5, NMO-unnumbered from Rickenbach) with the smallest extant representative *Dicerorhinus sumatrensis* (mean of MtIII L = 149.28, Guérin 1980; shoulder height of 1.30 m, Nowak 1999), *D. lamilloquense* (MtIII L = 112.5, NMO-unnumbered from Rickenbach) can be considered as even smaller. Its locomotion type was mediportal to graviportal (McIII GI = 0.281, Michel 1983; MtIII GI = 0.329, NMO-unnumbered from Rickenbach), close to the locomotion type of *Ceratotherium simum* (McIII GI = 0.300 and MtIII GI = 0.280, Guérin 1980). The hypsodonty index, calculated on an m3 from La Milloque (HI = 0.89; Michel 1983, tab. 8, pl. 3), is very close to the HI of *Ronzotherium romani* and corresponds also to a brachyodont dentition (Janis 1988). Based on direct observations of diacerathere skulls (*D. lemanense*, *D. asphaltense*, *D. aginense*), we assumed an intermediate head posture as in *Diceros bicornis*. According to Becker et al. (2009), the combination of intermediate head-holding with brachyodont teeth points to a rather high-level browser, probably well adapted to feed on high vegetation (Janis 1988; Becker et al. 2009).

By analogies with extant representatives and following the aforementioned anatomical type and the feeding behaviour, the rhinocerotids of Rickenbach represent sympatric species covering two ecologic types. Although the anatomic type of *Ronzotherium romani* is unknown today, the latter is considered a regular browser living in bushland, in the transitional zone between forest and grassland, like *Diceros bicornis* (Nowak 1999). Moreover, the cursorial locomotion type of *R. romani* suggests commonness in open areas. *Diaceratherium lamilloquense* corresponds to a regular-to-high browser living in dense or slightly open forests close to waterbeds or swamps. This habitat is somewhat comparable to those of *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis* (Nowak 1999).

Additionally, the sympatry of ronzotheres and diacerathes, already mentioned by Ménouret and Guérin (2009), is confirmed. According to the latter, the oldest record of this co-occurrence is dated to the earliest Chattian in St-André (MP26, France) and corresponds to the FAD of

the diaceratheres, with *Diaceratherium massiliae* (Ménouret and Guérin 2009). The locality of Rickenbach records here the youngest co-occurrence of these two rhinocerotids, which also corresponds to the LAD of the ronzotheres. To sum up, the co-occurrence, in Rickenbach, of *Ronzotherium romani* and *Diaceratherium lamilloquense* attests to a woodland-savannah landscape associated to patches of forested areas and tree-and-shrub savannah.

Comment on the rodents

Even though the ecologic value of the rodent must be discussed with prudence (most of the fossils correspond in fact to rejection pellets of birds, meaning that they were sorted by the predators' tastes), the rodents suggest a typical mixed association as well, with forests (attested by the presence of eomyids and castorids) and more open and/or arid environments (according to the theridomorphs).

Biogeochemistry

In their short synthesis on the rhinocerotids of Rickenbach, Emery et al. (2007) performed biogeochemical analysis on several mammalian teeth (Rhinocerotidae, Anthracotheriidae, Suoidea, and Ruminantia) coming from this locality. They analysed the carbon and oxygen stable isotopes of the carbonate fraction of tooth enamel. They obtained relatively homogeneous $\delta^{18}O_{CO3}$ values (from −5.4 to −3.0‰) amongst the ungulates from Rickenbach, and they calculated a mean annual temperature of nearly 20°C, corresponding to a subtropical climate (Emery et al. 2007). Surprisingly, the $\delta^{18}O_{CO3}$ values obtained from two ruminants are significantly higher (from −0.9 to −0.5‰) than the average covered by the mammalian community. Emery et al. (2007) hypothesised that either (1) these animals fed on leaves that underwent strong vapour transpiration, or (2) they drank water from a different area compared to the other mammals. A third explanation may be the sampling method. When analysing the total crown height for mean isotopic values, differences in the enamel isotopic composition may depend on the tooth considered and on its growing time (e.g., Bryant et al. 1996). Indeed, Merceron et al. (2006) proved the existence of seasonality by analysing two ruminants from the Late Miocene, and they observed similar differences in their $\delta^{18}O$ values. In Rickenbach, the small brachyodont-toothed ruminants probably needed only three to four months to form the enamel of their whole crown, contrarily to larger mammals that need almost a whole year. The higher $\delta^{18}O_{CO3}$ values displayed by the ruminants may indeed indicate a warmer season during which their teeth were formed compared to the mean $\delta^{18}O_{CO3}$ values of the entire community. This confirms the results obtained here from the cenogram, which supposes seasonality during the latest Oligocene.

General reconstruction

According to the aforementioned analyses, the palaeoenvironment of Rickenbach was probably a savannah woodland affected by a subtropical climate with clear seasonality. The mean annual temperature of around 20°C proposed by the biogeochemical analysis fits well with the floral assemblage, principally represented by palms and Lauraceous. The absence of taxads (joined to the presence of *Pinus)* may indicate a more arid environment as well.

The comparison of Rickenbach with other localities of the same age situated in the Swiss Molasse Basin shows that the palaeotopography of the basin certainly played an important role, both for flora and fauna. In the Subalpine Molasse (e.g., Rochette), the temperature was lower and the humidity clearly higher (Berger 1998). This was probably due to palaeoreliefs implying two main types of environments:

1. A humid swampy area along the early Alpine reliefs, marked by the deposit of the "Coal Molasse" (characteristic of the locality of Rochette),
2. A more arid and seasonal environment, marked by the deposit of lacustrine and evaporitic sediments in the distal part of the basin (e.g., "Calcaires delémontiens" and "Grès et Marnes gris à Gypse", Berger et al. 2005), sometimes drained by fluvial system ("Aarwanger Molasse", characteristic of the locality of Rickenbach).

The environment and climate of the latest Oligocene probably corresponded to the end of the Late Oligocene Warming (Zachos et al. 2001), right before the Mi-1 glaciation (Pekar et al. 2006). This period is marked by the "*Microbunodon* phase" of Stehlin (1922), dated to MP28-30, and the Rickenbach level corresponds to the beginning of the "Terminal Oligocene Crisis" (Becker et al. 2009), the faunal turnover "ETOFE-4" (Scherler 2011), and the phase "Extinction/Migration 3" observed from the ruminants (B. Mennecart, pers. obs.).

Conclusion

In this paper, we reassessed the faunal list of Rickenbach for the hoofed mammals. We described *Babameryx engesseri* gen. et sp. nov. (Ruminantia, Pecora), and highlighted for the first time the co-occurrence of *Diaceratherium lamilloquense* and *Ronzotherium romani* (Rhinocerotidae). We reconstructed the palaeoecology of the ungulates to determine the palaeoenvironment of Rickenbach as a savannah woodland affected by a subtropical climate with clear seasonality.

The present study emphasises the great interest of hoofed mammals for both biostratigraphy and palaeoecology.

These taxa underline the important place of the locality of Rickenbach in the understanding of the Late-Oligocene history. In this respect, the continuation of researches and new excavations are highly expected to highlight both the huge collection of the Naturmuseum Olten and the promotion of the Olten area to the public.

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